植 物 分 类 与 资 源 学 报 2013，35（5）：613～620
Plant Diversity and Resources DOI：10.7677/ynzwyj201312171

温度和湿度对草果花柱卷曲的影响*

杨耀文[1,2,3]，钱子刚[3]，李爱荣[1]，普春霞[1,2,3]，刘小莉[3]，管开云[1**]
（1 中国科学院昆明植物研究所，云南 昆明 650201；2 中国科学院大学，北京 100049；
3 云南中医学院中药材优良种苗繁育中心实验室，云南 昆明 650500）

摘要：草果（*Amomum tsaoko*）为姜科植物，有花柱卷曲机制。研究表明温度和湿度均影响草果上举型花和下垂型花的花柱卷曲，相对恒定的低温和高湿可促使花柱的同步卷曲。当8∶00-19∶30期间的平均温度小于18 ℃、平均湿度大于90%时，花柱卷曲没有滞后现象，卷曲的同步性较好。当平均温度大于18 ℃、平均湿度小于90%时，随着温度的升高和湿度的降低，花柱卷曲滞后愈加明显。和上举型花相比，下垂型花的花柱卷曲对湿度变化更为敏感；可能两种花型之间存在一定的分化。居群初花期19.17～19.52 ℃的平均温度和51.00%～51.44%的平均湿度，导致单朵下垂型花的寿命由1 d延长为2 d。温度和湿度变化对花柱卷曲的影响导致在居群水平上没有完全形成功能上的雌雄异株，可能影响草果的繁育和降低其适合度。从不同角度对花柱卷曲机制的深入研究，有助于更好的探索其起源和进化。

关键词：草果；温度；湿度；花柱卷曲；花期延迟
中图分类号：Q 944 **文献标识码**：A **文章编号**：2095-0845(2013)05-613-08

The Influence of Temperature and Humidity on Stylar Curvature in *Amomum tsaoko*（Zingiberaceae）*

YANG Yao-Wen[1,2,3], QIAN Zi-Gang[3], LI Ai-Rong[1], PU Chun-Xia[1,2,3], LIU Xiao-Li[3], GUAN Kai-Yun[1**]
（1 *Kunming Institute of Botany*, *Chinese Academy of Sciences*, Kunming 650201, China; 2 *University of Chinese Academy of Sciences*, Beijing 100049, China; 3 *The Center for Reproducing Fine Varieties of Chinese Medicinal Plants*, *Yunnan College of TCM*, Kunming 650500, China）

Abstract: Flexistyly is a floral mechanism involving extreme curving of the style first described in *Amomum tsaoko* Crevost & Lemarie. We examined the influence of temperature and humidity on stylar curvature in this species. Although floral behavior was similar to that reported previously in this species and other flexistylous gingers, there was a delay in stylar movement in two morphs, which differed strikingly from previous observations. When mean temperature and humidity between 8∶30 and 19∶30 hrs were below 18 ℃ and above 90%, respectively, style movement of both morphs was not delayed; however, there was a delay in style movement when temperature was increased above 18 ℃ and humidity fell below 90%. Stylar curvature of cataflexistylous flowers was more sensitive to change of humidity than anaflexistylous ones. When mean temperature and humidity were between 19.17-19.52 ℃ and 51.00%-51.44%, respectively, the anthesis of a single cataflexistylous flower was prolonged from 1 day to 2 days, and stylar curvature downwards was asynchronous. The asynchronous stylar movement did not ensure complete functional dioecy within a population, which would decrease successful cross-fertilization (outcrossing) between the two different

* Funding: Science and Technology Projects of Yunnan Province (2009CD078) and the Science Foundation of Yunnan Education Bureau (2010Z097)
** Author for correspondence; E-mail: guanky@mail.kib.ac.cn
Received date: 2012-12-17, Accepted date: 2013-02-21
作者简介：杨耀文（1967-）男，副教授，主要从事药用植物资源保护方面的教学和科研工作。E-mail：yangyaowen@mail.kib.ac.cn

forms, and affect the breeding and fitness of plants. Flexistyly is a special form of heterodichogamy, which requires further study to fully understand its origin and evolution.

Key words: *Amomum tsaoko*; Temperature; Humidity; Stylar movement; Prolonged flowering

Flexistyly is a unique and motile sexual dimorphism first found in *Amomum tsaoko* Crevost & Lemarie (Cui *et al.*, 1995a, b) and then in *Alpinia* Roxb. species (Li *et al.*, 2001a, b, 2002; Zhang *et al.*, 2003; Takano *et al.*, 2005; Wang *et al.*, 2005a, b). In a flexistylous species, there are two floral morphs (anaflexistylous and cataflexistylous) with styles behaving oppositely and differing in the time of stigma receptivity and pollen release during anthesis. Through active stylar curvature, each morph changes from one sexual phase to the other in the middle of the 1-d flowering period, and the two morphs form a reciprocal cooperation between stigmas and anthers to promote outcrossing (Li *et al.*, 2001a; Zhang and Li, 2002). The sexual organs are separated temporarily and spatially by active stylar curvature, thus interference of male and female functions may reduce to small extent (Li *et al.*, 2001a, b; Barrett, 2002; Zhang and Li, 2002; Zhang *et al.*, 2003; Zhang, 2004).

As a special form of heterodichogamy, flexistyly mechanism was observed in several genera of Zingiberaceae, such as *Alpinia*, *Amomum*, *Etlingera*, and *Paramomum* (Ren *et al.*, 2007). This mechanism was found in all *Alpinia* species which have been observed so far; however, not all species in *Amomum* have this mating strategy. Therefore, *Amomum* is an ideal model for discussing flexistyly phylogeny and flexistyly in this genus is worth to be studied in details (Ren *et al.*, 2007). Weather condition affected the speed of stylar movement of *Alpinia* species (Li *et al.*, 2001a). Rainy weather would delay the stylar movement of *Alpinia* (Zhang and Li, 2002). These researches imply that temperature and humidity would influence the stylar movement. The influence of weather conditions on the flexistylous movement of style of *A. tsaoko* has not been reported yet. To fully understand the origin and evolution of this unique floral mechanism, studying flexistyly in *Amomum* from various aspects are need. In this sense, we reported the influence of temperature and humidity on the stylar movement of *A. tsaoko*, and also discussed its effect on the breeding of this species in this research.

1 Material and method

1.1 Research species

Amomum tsaoko Crevost et Lemaire is a perennial herb of Zingiberaceae, usually 2–3 m in height. Inflorescence consists of a densely flowered spike that arises from rhizomes. The showy yellow labellum with red nectar guide is fused with the single stamen to form a tube, the free part of which forms an expanded landing platform for visitors. An apparent anther appendage (ca. 4 mm×11 mm) forms an arch at the top of the anther and surrounds the stigma. Flowering occurs from April to June, capsules are ripe from September to December (Wu and Raven, 2000).

Amomum tsaoko distributes in Yunnan Province, southwest China (Wu and Raven, 2000), but now its wild (or natural) population is almost extinct in Yunnan. Since its fruit is used as common materia medica (Chinese Pharmacopoeia Commission, 2010) and a food condiment in China, it is cultivated as economic plant in Yunnan.

1.2 Study site

The study was conducted from 24 to 26 in May, 2007, and from 10 to 13 in May, 2009, at the Gaoligong Mountain, Yunnan Province, southwest China. In the study site, primary forest is kept as a part of natural reserve, and *A. tsaoko* inhabits understory of broad-leaved forest and its fruits are collected by local villagers. Population 1 (24°50.289′ N, 98°46.501′ E, 2 070 m in altitude) is about 3 km away from population 2 (25°3.702′ N, 98°30.129′E,

2 219 m in altitude). Both populations have been cultivated for more than 20 years. Flowering of population 1 and 2 occurred from late April to early June and from early May to June, respectively.

1.3 Field observations

In the two populations, all flowers that randomly selected from two morphs were subjected to observations. For each flower, the following traits were observed and recorded every 30 min from 08:30 to 19:30: movement of style (upward or downward curving), position of stigma (above or below anther) and anther dehiscence.

We observed 243 flowers from 23 individuals, including 117 flowers from 10 cataflexistylous individuals and 126 flowers from 13 anaflexistylous individuals, respectively. In population 1, we observed four individuals of each morph and 57 flowers (22 anaflexistylous flowers +35 cataflexistylous flowers) over three days in 2007. Two to four flowers were selected at random from the same individual and observed every day. Nine anaflexistylous individuals and 104 flowers from these individuals were observed over two days in 2009. Six to ten flowers were selected at random every day. In population 2, there were only 6 cataflexistyled individuals that came into anthesis on May 10–11, 2009, there were 60 open flowers on May 10, and 22 open flowers on May 11.

The temperature and humidity were monitored and recorded every 30 min at the center of each population, of where the degree of shading was moderate and presenting the average level of temperature and humidity across population.

1.4 Statistical analyses

Frequency of stylar movement of the same morph in different time of one-day anthesis was counted out by proportion of flowers which stylar movement had occurred to the total flowers observed in corresponding time. The style of both floral morphs didn't obviously curve downwards or upwards until 19:30, the stigma was still above the anther and wasn't in its receptive position (for cataflexistylous morph), or the stigma was still below the anther and wasn't far away from the insect visiting channel (for anaflexistylous morph), which were termed delay of stylar movement. Percentage of stylar delay of the same floral morph in one-day anthesis was counted out by proportion of flowers which stylar movement delayed to the total flowers observed.

Date on temperature and humidity were checked by Homogeneity of variance test, then compared by one-way analysis of variance (ANOVA) in SPPS (13.0 version). Student Newman Keuls Test (S-N-K test) was used to analyze the variances among the seven days. Correlation was tested by Bivariate Correlation and Partial Correlate in SPSS (13.0 version).

2 Results

2.1 Significant difference of temperature and humidity

Homogeneity of variance test showed that the variances of both temperature and humidity were equal ($P=0.000<0.01$). Among the seven days, both temperature ($df=6$, $F=13.170$, $P=0.000$) and humidity ($df=6$, $F=68.161$, $P=0.000$) from 8:30 to 19:30 were significant different. By S-N-K test ($\alpha=0.05$), the temperature and humidity of these days were divided into 4 and 3 subsets respectively (Table 1).

2.2 Stylar movement and prolonged flowering

Despite the resemblance in floral behavior there were still some differences between the previous studies and ours. In population 1, both floral morphs changed asynchronously from one sexual stage to another on May 24–26, 2007 (Fig. 1). The analogous phenomena were also observed on May 12 and 13, 2009, the styles of anaflexistyled flowers didn't bend upward strictly synchronously on the same day (Fig. 2). In population 2, we observed that the longevity of a single cataflexistyled flower was lengthened from 1 d to 2 d, and their corollas withered and closed till 11:00–13:00 of the next day. The most cataflexistyled flowers opened on May 10 were in their male stage on the first day (May 10) because their styles

remained upwards, and their styles curved downwards and they were in their female stage on the second day (May 11). The same case was observed in flowers opened on May 11. In the process of these cataflexistyled flowers opening, their styles curved downwards asynchronously on the same day (Fig. 3).

Although the styles of two morphs didn't curve strictly simultaneously during our observation days (2007 and 2009), there was a time when the styles curved convergently. The styles of anaflexistyled flowers curved upwards mainly from 16:00 to 18:30, and styles of cataflexistyled flowers curved downwards mainly from 15:30 to 16:00 and from 17:30 to 19:30 (Fig. 1-3).

Delay of stylar movement was observed in the five days with exception of May 24 and May 26. The delay of stylar movement of two morphs was more serious in 2009 than 2007, with significant difference of both temperature and humidity between these two years (Table 1).

Table 1 Delay of stylar movement and the changes of temperature and humidity during the field observations

Day	Percentage of stylar delay of anaflexistylous flower/%	Percentage of stylar delay of cataflexistylous flower/%	8:00-19:30			
			Temperature/℃		Humidity/%	
			(Mean±*SD*)	Subset (α=0.05) by S-N-K test	(Mean±*SD*)	Subset (α=0.05) by S-N-K test
May 24, 2007	0.00	0.00	16.65±1.03	1	95.74±0.81	3
May 26, 2007	0.00	0.00	17.22±1.59	1	90.87±6.86	3 or 2
May 25, 2007	14.29	4.76	18.13±1.58	1 or 2	87.22±4.82	2
May 11, 2009	data missing	77.27	19.52±3.29	2 or 3	51.44±13.19	1
May 10, 2009	data missing	83.33	19.17±2.85	2 or 3	51.00±14.05	1
May 13, 2009	21.74	data missing	21.04±2.98	3 or 4	57.26±14.42	1
May 12, 2009	25.71	data missing	22.35±4.12	4	55.91±17.84	1

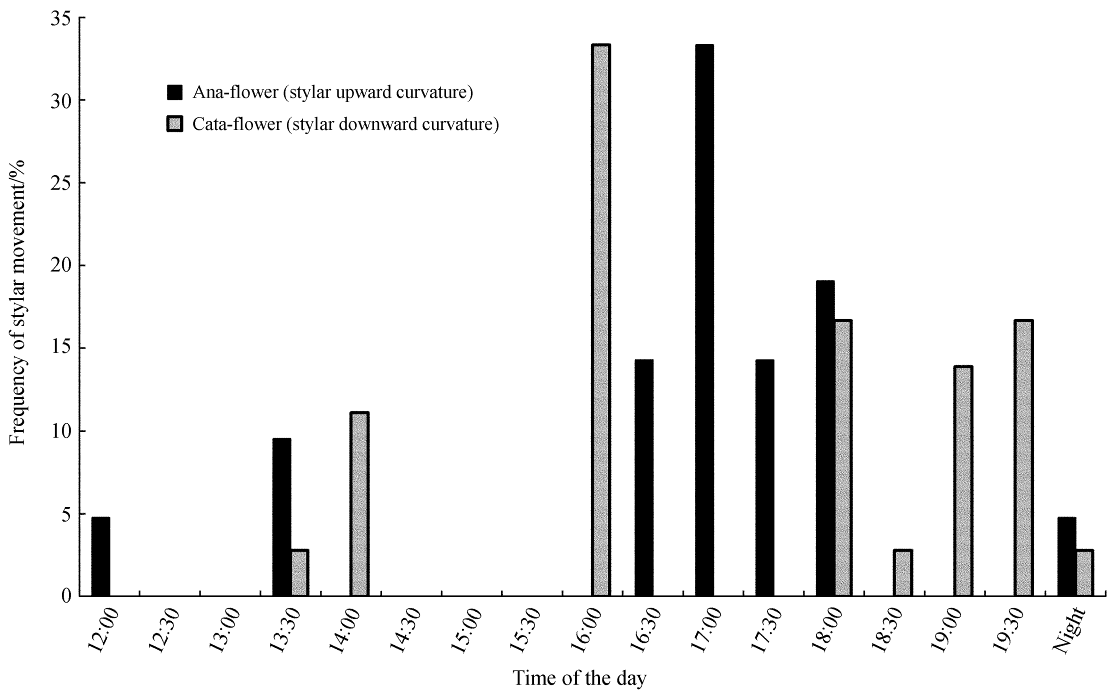

Fig. 1 The frequency of stylar movement of *A. tsaoko* during 1-d anthesis (May 24-26, 2007)

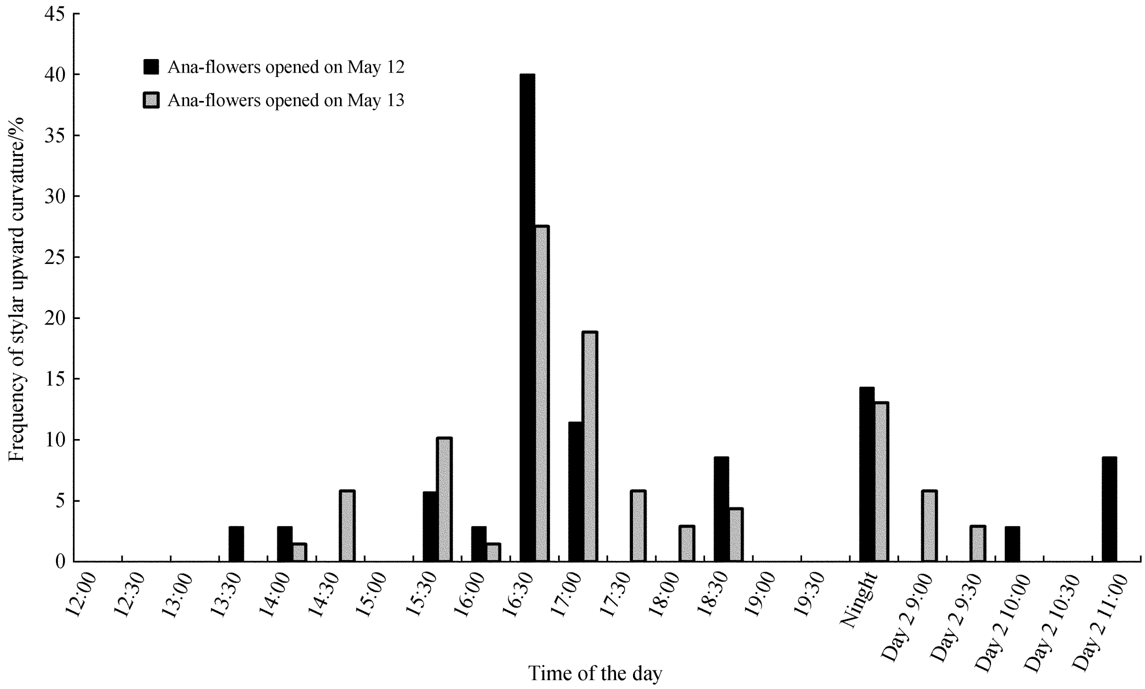

Fig. 2　The frequency of stylar upward curvature of the anaflexistyled flowers during 1-d anthesis (May 12–13, 2009)

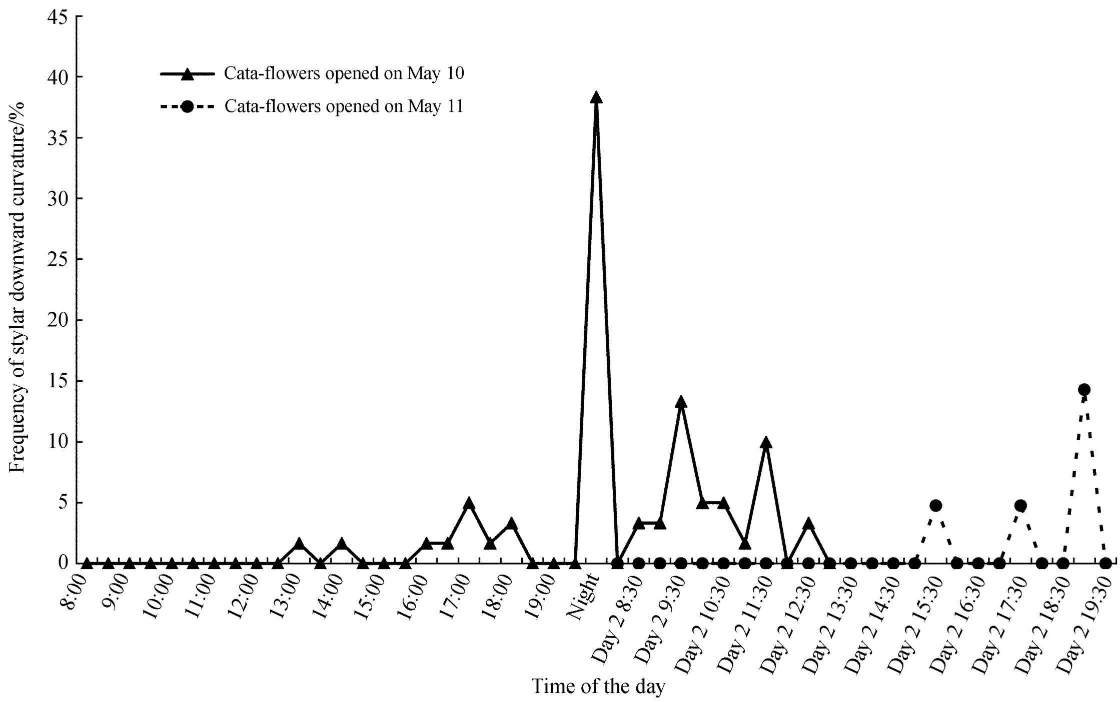

Fig. 3　The frequency of stylar downward curvature of the cataflexistyled flowers and prolonged flowering (May 10–11, 2009)

2.3　Influence of temperature and humidity on stylar movement

The result of Bivariate Correlation analysis indicated that significant correlations occurred between percentage of stylar delay of anaflexistylous flower and some climatic factors, viz. mean temperature from 8:30 to 19:30 ($df=3$, $r=0.948$, $P=0.014<0.05$), standard deviation of temperature ($df=3$, r

$=0.886$, $P=0.046<0.05$), and mean humidity from 8∶30 to 19∶30 ($df=3$, $r=-0.921$, $P=0.026<0.05$). Accordingly, significant correlations were tested out between percentage of stylar delay of cataflexistylous flower and some climatic factors, viz. mean temperature from 8∶30 to 19∶30 ($df=3$, $r=0.918$, $P=0.028<0.05$), standard deviation of temperature ($df=3$, $r=0.953$, $P=0.012<0.05$), mean humidity from 8∶30 to 19∶30 ($df=3$, $r=-0.994$, $P=0.001<0.01$), standard deviation of humidity ($df=3$, $r=0.924$, $P=0.025<0.05$).

The result of Partial Correlation analysis indicated that significant correlations occurred between percentage of stylar delay of cataflexistylous flower and mean humidity from 8∶30 to 19∶30 ($df=2$, $r=-0.989$, $P=0.011<0.05$) by control variable of mean temperature.

3 Discussion

There are numerous examples of floral or reproductive polymorphisms maintained within a population (Pannell *et al.*, 2005), displaying diverse strategies of plant reproduction (Barrett, 2002). Flexistyly is a genetic polymorphism to promote outcrossing and reduce interference between male and female function through active stylar curvature. When stigma was already located above the anther, the flower was in its male stage, oppositely while stigma was below the anther, the flower was in its female stage. Both floral morphs change almost synchronously from one sexual stage to another without gender overlap (Ren *et al.*, 2007), exhibiting temporal dioecy, which prevents not only self-pollination within a flower and within the same inflorescence, but also among individuals of the same floral morph in a population, thus in natural condition, pollination can only occur between different morphs (Ren *et al.*, 2007). Sex expression enhances sexual reproduction through an optimal model of bisexual resource allocation (Charnov, 1979). For a flexistylous ginger, the stylar movement seems to play an important role during the bisexual resource allocation, and the speed of stylar movement is an important factor in the process.

By comparison of the analysis results, the stylar movement was more synchronous from May 24–26, 2007 than from May 10–13, 2009; the stylar movement was more asynchronous on May 25 than May 24 and May 26. Both temperature and humidity were significantly different among these days. The correlation analysis indicated that change of the temperature and humidity from 8∶30 to 19∶30 would influence the stylar movement. When the mean temperature from 8∶30 to 19∶30 was below 18 ℃, the style movement of both morphs didn't delay. When the mean temperature was above 18 ℃, the stylar movement of two morphs delayed, and more high the mean temperature, the more delay of the stylar movement. When the mean humidity from 8∶30 to 19∶30 was above 90%, the stylar movement of two morphs didn't delay. When the mean humidity was below 90%, the stylar movement of both morphs delayed, and more lower the mean humidity, the more delay of the stylar movement.

If the style of cataflexistylous flower didn't bend downward to its receptive position until 19∶30, opportunity of the stigma accepting pollen would be greatly reduced. Since the stigma of anaflexistylous flower was already located above the anther, far from the insect visiting channel, then its pollen sacs began to dehisce; if the style of anaflexistylous flower didn't curve above the anther until 19∶30, opportunity of the pollen releasing from anther would also be greatly reduced, and the pollen would fall and accumulate on the labellum when we tore open these faded flowers in the next morning. Delay of stylar movement was more obvious and asynchronization of stylar movement was more serious. Our studies indicated that both temperature and humidity affected the stylar movement of both floral morphs of *A. tsaoko*, displaying a tendency that steady low temperature (<18 ℃) would lead the stylar movement toward more synchronization than the mean temperature of 18–22 ℃, and steady high humidity (>90%) would

lead the stylar movement toward more synchronization than changeable low humidity (<58%).

The similar asynchronous stylar movement was reported in *Alpinia hainanensis* (Wang *et al.*, 2005a). The asynchronous stylar movement of *A. tsaoko* might be caused by photoperiod (Cui *et al.*, 1995a). Different light intensity and duration would cause different temperature and humidity. The degree of shading was changing across a day, which would result in alteration of temperature and humidity within population. During field observations, we observed that the stylar movement was more asynchronous on the sunny days than the cloudy days, because the heterogeneity of environmental factors across the same population was smaller on cloudy day than sunny day.

The synchronous stylar movement ensured that there was completely functional dioecy within a population, which insured successful cross-fertilization (outcrossing) only occurs between the two different forms (Li *et al.*, 2001a). Synchronous stylar movement of a flexistylous species could increase pollen export during their male phase by reducing levels of within- and between-flower interference (Sun *et al.*, 2011). Cui *et al.* (1996) indicated that *A. tsaoko* was self-compatible. Self-fertilization would lead to inbreeding depression due to expression of deleterious recessive genes (Charlesworth and Charlesworth, 1987, 1999). The peak of stylar movement of the two morphs would promote that the outcrossing would occur mainly between the two different forms. The heterogeneity of environmental factors in a population could cause some asynchronous stylar movement, which would influence on the breeding of population, and discount fitness of the plant.

Style movement appeared to have asymmetrical effects, in contrast to male function, female function appeared to be affected weakly by stigma movement (Sun *et al.*, 2007, 2011). The analysis also indicated that the stylar movement of the cataflexistylous flowers was more sensitive to change of humidity than the anaflexistyled ones. There might be some differentiation between the two morphs. The fruit set of the anaflexistylous individual was significantly higher than the cataflexistylous one (unpublished observation). It was likely correlative of the differentiation between the two morphs. Both stylar movement and breeding of the cataflexistylous morph appeared to be affected greatly by weather condition in contrast to the anaflexistylous morph.

The sex expression of plants was regarded as a quantitative character, which was termed as phenotypic gender and functional gender, phenotypic gender was usually measured by the morphological feature of flowering (Lloyd, 1979). Floral longevity was assumed to reflect a balance between the benefit of increased pollination success and the cost of flower maintenance (Ashman and Schoen, 1994; Schoen and Ashman, 1995), and long floral longevity was advantageous to both female and male fitness in *Hedychium villosum* var. *villosum* (Gao *et al.*, 2009). Reproductive assurance would be a self-protecting mechanism or strategy (Baker, 1955). In population 2, all the flowers were cataflexistylous during the early flowering, both temperature (19.17–19.52 ℃) and humidity (51.00–51.44%) might influence on the floral behavior: the anthesis of a single flower was prolonged from 1 d to 2 d, and their stylar downward movement was asynchronous. These cataflexistyled flowers mainly acted as functionally male flowers at the first day, and as functionally female flowers at the second day; outcrossing would occur between the same morphs for reproductive assurance. So the prolonged flowering would help to improve the both of female and male fitness for reproductive assurance on special occasions. Although the similar example was reported in *Alpineae oxyphylla* (Wang *et al.*, 2005b), it was observed for the first time in *A. tsaoko*.

Heterodichogamy is understood to come from synchronous dichogamy and is heading towards dioecy (Renner, 2001). Flexistyly is a special heterodichogamy, further insight into which would be worth studying in details to fully understand its origin and evolution.

Acknowledgements: We thank Dr. Yu Wen-bin for his critical reading of the paper and good advice.

References:

Ashman TL, Schoen DJ, 1994. How long should flowers live? [J]. *Nature*, **371**: 788—791

Baker HG, 1955. Self-compatibility and establishment after "long distance" dispersa1 [J]. *Evolution*, **9**: 347—349

Barrett SCH, 2002. The evolution of plant sexual diversity [J]. *Nature Reviews Genetics*, **3**: 274—284

Charlesworth B, Charlesworth D, 1987. A model for the evolution of dioecy and gynodioecy [J]. *American Naturalist*, **112**: 975—997

Charlesworth B, Charlesworth D, 1999. The genetic basis of inbreeding depression [J]. *Genetic Research*, **74**: 329—340

Charnov EL, 1979. Simultanous hermaphroditism and sexual selection [J]. *Proceedings of the National Academy of Sciences of the United States of America*, **76**: 2480—2484

Chinese Pharmacopoeia Commission (中国药典委员会), 2010. *Pharmacopoeia of the People's Republic of China* (Vol.1) [M]. Beijing: Chinese Medicine Science and Technology Press, 222—223

Cui XL (崔晓龙), Wei RC (魏蓉城), Huang RF (黄瑞复), 1995a. A preliminary study on the genetic system of *Amomum tsaoko* [J]. *Journal of Yunnan University* (Nat. Sci.) (云南大学学报(自然科学版)), **17**: 290—297

Cui XL (崔晓龙), Wei RC (魏蓉城), Huang RF (黄瑞复), 1995b. Study on the artificial population structure of *Amomum tsaoko* [J]. *Southwest China Journal of Agricultural Science* (西南农业学报), **8** (4): 114—118

Cui XL (崔晓龙), Wei RC (魏蓉城), Huang RF (黄瑞复), 1996. Biological characters of flowering and fruiting habit in *Amomum tsaoko* [J]. *Southwest China Journal of Agricultural Sciences* (西南农业学报), **9** (1): 109—113

Gao JY (高江云), Yang ZH (杨自辉), Li QJ (李庆军), 2009. Effects of floral longevity on male and female fitness in *Hedychium villosum* var. *villosum* [J]. *Chinese Journal of Plant Ecology* (植物生态学报), **33** (1): 89—96

Li QJ, Xu ZF, Kress WJ *et al*., 2001a. Flexible style that encourage outcrossing [J]. *Nature*, **410**: 432

Li QJ (李庆军), Xu ZF (许再富), Kress WJ *et al*., 2001b. Study on the flexistyly pollination mechanism in *Alpinia* plants (Zingiberaceae) [J]. *Acta Botanica Sinica* (植物学报), **43**: 346—369

Li QJ, Kress WJ, Xu ZF *et al*., 2002. Mating system and stigmatic behaviour during flowering of *Alpinia kwangsiensis* (Zingiberaceae) [J]. *Plant Systematics and Evolution*, **232**: 123—132

Lloyd DG, 1979. Parental strategies in angiosperms. In: International Symposium on Reproduction in Flowering Plants [J]. *New Zealand Journal of Botany*, **17**: 595—605

Pannell RJ, Dorken EM, Eppley MS, 2005. 'Haldane's Sieve' in a metapopulation: sifting through pl. reproductive polymorphisms [J]. *Trends in Ecology & Evolution*, **20**: 374—379

Ren PY, Liu M, Li QJ, 2007. An example of flexistyly in a wild cardamom species *Amomum maximum* (Zingiberaceae) [J]. *Plant Systematics and Evolution*, **267**: 147—154

Renner SS, 2001. How common is heterodichogamy? [J]. *Trends in Ecology & Evolution*, **16**: 595—597

Schoen DJ, Ashman TL, 1995. The evolution of floral longevity: resource allocation to maintenance versus construction of repeated parts in modular organisms [J]. *Evolution*, **49**: 131—139

Sun S, Gao JY, Liao WJ *et al*., 2007. Adaptive significance of flexistyly in *Alpinia blepharocalyx* (Zingiberaceae): a hand-pollination experiment [J]. *Annals of Botany*, **99**: 661—666

Sun S, Zhang DY, Ives AR *et al*., 2011. Why do stigmas move in a flexistylous plant? [J]. *Journal of Evolutionary Biology*, **24**: 497—504

Takano A, Gisil J, Yusoff M *et al*., 2005. Floral and pollinator behaviour of flexistylous *Bornran ginger*, *Alpinia nieuwenhuizii* (Zingiberaceae) [J]. *Plant Systematics and Evolution*, **252**: 167—173

Wang YQ (王英强), Zhang DX (张奠湘), Chen ZY (陈忠毅), 2005a. Pollination biology of *Alpinia hainanensis* (Zingiberaceae) [J]. *Acta Phytotaxonomica Sinica* (植物分类学报), **43** (1): 37—49

Wang YQ (王英强), Zhang DX (张奠湘), Chen ZY (陈忠毅), 2005b. A preliminary study of the pollination biology of *Alpinia oxyphylla* (Zingiberaceae) [J]. *Acta Phytoecologica Sinica* (植物生态学报), **29** (4): 599—609

Wu ZY, Raven PH eds., 2000. *Flora of China* [M]. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press, **24**: 325

Zhang L (张玲), Li QJ (李庆军), 2002. Flexistyly and its evolutionary ecological significance [J]. *Acta Phytoecologica Sinica* (植物生态学报), **26**: 385—390

Zhang L, Li QJ, Deng XB *et al*., 2003. Reproductive biology of *Alpinia blepharocalyx* (Zingiberaceae): another example of flexistyly [J]. *Plant Systematics and Evolution*, **241**: 67—76

Zhang DY (张大勇), 2004. *The Evolution of Plant Life History and Reproductive Ecology* [M]. Beijing: Science Press